First glimpse into Lower Jurassic deep-sea biodiversity: *in situ* diversification and resilience against extinction

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Owing to the assumed lack of deep-sea macrofossils older than the Late Cretaceous, very little is known about the geological history of deep-sea communities, and most inference-based hypotheses argue for repeated recolonizations of the deep sea from shelf habitats following major palaeoceanographic perturbations. We present a fossil deep-sea assemblage of echinoderms, gastropods, brachiopods and ostracods, from the Early Jurassic of the Glasenbach Gorge, Austria, which includes the oldest known representatives of a number of extant deep-sea groups, and thus implies that *in situ* diversification, in contrast to immigration from shelf habitats, played a much greater role in shaping modern deep-sea biodiversity than previously thought. A comparison with coeval shelf assemblages reveals that, at least in some of the analysed groups, significantly more extant families/superfamilies have endured in the deep sea since the Early Jurassic than in the shelf seas, which suggests that deep-sea biota are more resilient against extinction than shallow-water ones. In addition, a number of extant deep-sea families/superfamilies found in the Glasenbach assemblage lack post-Jurassic shelf occurrences, implying that if there was a complete extinction of the deep-sea fauna followed by replacement from the shelf, it must have happened before the Late Jurassic.

1. Introduction

Thanks to intense research efforts during the last few decades, it is now generally acknowledged that the deep sea supports one of the highest levels of biodiversity on Earth, while differing fundamentally from shallow marine and terrestrial ecosystems [1,2]. Yet, the evolutionary processes that have shaped the unique attributes of the deep sea are still controversial. Growing evidence that the deep sea was anything but stable and unchanging through time has challenged the initial concept of the deep sea as a refuge for ancient lineages excluded from shelf habitats. Debates have focused on the impact of variations in temperature, oxygenation and circulation mode on the colonization of deep habitats, and at least for the late Cenozoic, deep-sea sediment cores have provided extensive benthic foraminifer and ostracod microfossil evidence in this respect [3,4]. Biogeographic patterns and molecular clock estimates have yielded dates which predominantly converge to a latest Mesozoic or early Cenozoic origin of the modern deep-sea fauna [5–9]. Testing these hypotheses and exploring older deep-sea biodiversity using direct fossil evidence, however, has been hampered so far by the sparse record of
deep-sea faunas older than the Late Cretaceous [6]. The recent discovery of a modern-type echinoderm assemblage from Lower Cretaceous bathyal deposits of the subtropical north Atlantic [10] demonstrated that direct fossil evidence of deep-sea biodiversity exists in sediments beyond Late Cretaceous age and showed that the origin of at least some modern deep-sea groups is to be sought in even older strata.

2. Geological context

We here present fossil remains of a newly discovered diverse deep-marine assemblage retrieved from marls of the Kehlbach and Scheck Members (informally known as ‘Hauptknollenbrekzie’) within the Adnet Formation, exposed in the Glasenbach Gorge, south of Salzburg in the northern Calcareous Alps, Austria. These sediments are interpreted as a giant slump deposit derived from the slope of a submarine high in the former northern Tethys Ocean, and their ammonite fauna indicates an Early Jurassic age (from the late Sinemurian Echioceras raricostatum Zone to the late Pliensbachian Anomaloceras marginatum Zone) [11,12]. Palaeo-depth reconstructions suggest at least 1000 m for the slump components, based on subsidence models of the area, sedimentological comparisons with present-day equivalents and the presence of very similar lithologies directly overlying both oceanic and deeply submerged continental crust in the Jurassic of the north Atlantic [11,13], as well as the absence of light-dependent benthic organisms even on the submarine tops of the source area of the slumping mass [12]. These estimates are supported by our palaeobathymetric analysis using microbioerosion trace fossils in 15 bivalve and brachiopod shell fragments and belemnite rostra. Not a single unequivocal trace of a phototrophic chlorophyte or cyanobacterium, which could indicate a photic environment, was found. Rather, all identified traces are produced by heterotrophic organisms (mostly marine fungi) and are typical constituents of aphotic trace fossil assemblages (figure 1) [14]. Thus, the material studied herein must have been deposited at a palaeo-depth exceeding the lower limit of sunlight influence in the water column, which, in the present case (low palaeo-latitude sea with low water turbidity, deduced from the low sedimentation rate [11]), was between 150 m (deepest regular phototrophic records during settlement experiments [15]) and 370 m (deepest known occurrence of phototrophic microendoliths [16]), and thus well below regular palaeo-shelf depths.

Further evidence supporting a bathyal palaeo-depth is provided by the ostracod assemblage of the Glasenbach fauna, which includes only forms lacking eyes or other signs of

Figure 1. Scanning electron microscope images of microboring trace fossils (in order of abundance) prepared as epoxy resin casts from mollusc shells from the Sinemurian–Pliensbachian (Early Jurassic) of the Glasenbach section, Austria. (a) Semi-cylindrical resin cast of a belemnite rostrum exhibiting a large number of microborings; (b) the dominant fungal microboring Polyactina araneola, in modern seas produced by the fungus Conchyliastrum; (c) the aphotic index ichnotaxon Orthogonum lineare, producer unknown but most likely a fungus; (d) cluster of Flagrichnus profundus, produced by schizochytrid fungi; (e) Orthogonum giganteum, producer unknown; (f) Saccomorpha isp., presumed fungal trace; (g) Podichnus centrifugalis, attachment scar of a juvenile brachiopod pedicle; (h) Platydendrina convexa, producer unknown; (i) unknown dichotomously branching dendritid microboring with affinity to the ichnogenus Abeliella. Scale bars equal 1 mm in (a), 10 μm in (b,d,f) and 100 μm in (c,e,g–i).
photoreception. In addition, it almost exclusively consists of members of the extant eurybathic Bairdioidea, and thus fundamentally differs from all known coeval ostracod assemblages from shelf depths \[17,18\] and instead resembles a coeval assemblage found in slope deposits from Turkey \[19\]. The Glasenbach assemblage thus provides a unique window into Early Jurassic deep-sea biodiversity and predates the late Mesozoic oceanic anoxic events commonly considered to have triggered extinction in the deep sea and subsequent replacement from the shelf.

3. Material and methods
Specimens were collected in the field or picked from washed residues. Figured specimens were deposited at the Natural History Museum in Vienna. Families and, where applicable, superfamilies were chosen as basis for the faunal analyses because they were found to represent a compromise between taxonomic resolution and comparability with modern communities. Identifications of dissociated echinoderm plates followed latest taxonomic recommendations \[20–22\].

To assess the origin, resilience and bathymetric range shifts of the deep-sea fauna, we classified the families/superfamilies of the Glasenbach assemblage as well as coeval shelf (less than 200 m palaeo-depth) faunas \[20,21,23–36\] as extinct, or extant and, according to their present-day bathymetric distribution, typically deep, typically shallow, or without depth preference (eurybathic) (figure 3; electronic supplementary material, table 1). Our bathymetric classification was based on the averaged mean depth distribution of the extant species of the families/superfamilies (calculated by averaging the upper and lower distribution boundaries for each species and by computing the arithmetic mean of the obtained values for each family/superfamily): typically deep—averaged mean depth greater than 500 m; typically shallow—averaged mean depth shallower than 200 m; eurybathic—averaged mean depth between 200 and 500 m. The upper boundary of the deep sea is commonly set between 200 and 500 m, in line with the fading of seasonal variations in physical parameters (e.g. temperature) and of the influence of sunlight \[2,6,37–39\]. We adopted a conservative approach using the 500 m boundary to minimize the impact of potential outliers from shelf depths. Microbioerosion trace fossils were analysed by applying the vacuum cast-embedding method and scanning electron microscopic imaging to visualize the delicate microborings in decalcified polymer-resin casts \[14\]. Statistic tests were performed using the software package PAST v. 2.13 \[40\].

4. Results and discussion
Among the several thousand available specimens, we distinguished at least 68 species belonging to four different phyla, i.e. echinoderms (ophiuroids, asteroids, echinoids and crinoids), molluscs (gastropods), brachiopods and crustaceans (ostracods) (figure 2 and electronic supplementary material).

This assemblage includes the extant, typically deep ophiomy cetid ophiuroids, basal pterasterid asteroids and gwynioid brachiopods. These fossils predate the hitherto oldest record of these groups from Middle Jurassic shallow-water deposits by more than 25 Myr \[20,21,23,24\]. In addition, four extant deep-sea groups present in the Glasenbach assemblage, namely benthopectinid asteroids, eudesicrinid crinoids and (a) Eudesicrinus cuneatus (Eudesicrinidae, Crinoidea), cup in lateral view; (b) Benthopectinidae (Asteroidea) new genus and species, ambulacral in actinal view; (c) Pterasteridae (Asteroidea) genus and species indeterminate, ambulacral in actinal view; (d) Aspidodiadematidae (Echinoidea) new genus and species, test in latero-oral view; (e) Ophiomyctidae (Ophiuroidea) new genus and species, lateral arm plate in external view; (f) Securithyris adnethensis (Dyscolioidea, Rhynchonellata), in dorsal view; (g) Zellania sp. (Gwynioidea, Rhynchonellata), in dorsal view; (h) Pleurotomarioidea (Gastropoda) genus and species indeterminate. Scale bars equal 500 μm (a–d, f–g), 200 μm (e) and 1000 μm (h).
We show for the first time, to our knowledge since the Early Jurassic: the potential to generate higher-level evolutionary stability than shallow-water environments, and second that bathymetric shifts, in contrast to bathymetric extensions, from the deep sea to shallow waters are unlikely. Many extant deep-sea families/superfamilies present in the Glasenbach assemblage occur also in Early Jurassic shallow-water settings. Their restriction to the deep sea today thus results from a restriction of their once broad bathymetric range. This loss of shallow-water representatives among the once eurybathic groups seems to be a continuous process through geological time [43], as suggested by the last shelf occurrences of some of the Glasenbach families/superfamilies: e.g. Eudesicrinidae in the Late Jurassic [21], Zeillerioidea in the Early Cretaceous [23], and Pleurotomarioidea in the Cenozoic [44].

Several present-day deep-sea families, including Benthopetocinidae, Aspidodiadematidae, Eudesicrinidae and Ophiomycetidae, lack a post-Jurassic fossil record at shelf depths but were already present in the Early Jurassic Glasenbach deep-sea assemblage. Had there been a complete extinction of the deep-sea fauna followed by recolonization from shelf seas since the Early Jurassic [1,5], it must have happened before the Late Jurassic. This further highlights the resilience of the deep sea against major palaeoceanographic perturbations and sheds further doubt on the global extent and/or devastating nature of the so-called anoxic events during the late Mesozoic [10,45–47].

5. Conclusion

In summary, our results imply that two macroevolutionary processes have concurrently contributed to deep-sea biodiversity since the Early Jurassic: the potential to generate higher-level taxonomic diversity and resilience against major palaeoceanographic perturbations. We show for the first time, to our
knowledge, that higher level taxa can originate in the deep sea, expand to shelf depths and survive in the deep sea even after having gone extinct in the shallow seas again. We speculate that the resilience of the deep sea results from the sheer size of the environment combined with the great dispersal potential of the deep-sea benthos, increasing the chance for taxa to survive in deep-sea refuges and to subsequently re-expand. The potential to generate diversity might result from the many unique attributes of the deep-sea environment [2], which require unique adaptations that can only evolve in situ. Whatever the causes, our results shed new light on the role of the deep sea as a macroevolutionary source and reservoir of biodiversity, as well as on its potential to contribute to shallow-water diversity.

The latter point in particular calls for a careful reappraisal of the impact of deep-sea trawling and mining activities on marine biodiversity.

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